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GEOGRAPHIC VARIATION IN THE FREQUENCIES OF TRICHOME PHENOTYPES OF *DATURA WRIGHTII* AND CORRELATION WITH ANNUAL WATER DEFICIT

J. DANIEL HARE[1] AND ELIZABETH ELLE[2]
Department of Entomology, University of California, Riverside, CA 92521

ABSTRACT

The perennial plant species, *Datura wrightii* Regel (Solanaceae) is dimorphic for leaf trichome type. Some plants produce almost exclusively short, non-glandular trichomes, while other plants within the same population produce almost exclusively longer, glandular trichomes. In a previous survey of 19 southern California populations, the frequency of plants producing glandular trichomes ranged from 0–82%, and plants with glandular trichomes were absent from desert populations. Here we expand our studies to a total of 56 *D. wrightii* populations from central and southern California. We also examined the relationship between the frequency of glandular trichomes and two factors that broadly determine the availability of water at each site. The first was mean annual rainfall, while the second was mean annual evapotranspiration rate. The frequency of plants with glandular trichomes increased with increasing mean rainfall and decreased with increasing mean annual evapotranspiration rate. Combined, these two environmental variables accounted for about one-third of the variation in the proportion of plants with glandular trichomes. Results suggest that the production of a water-based exudate by plants with glandular trichomes may impose an additional demand for water on those plants compared to plants with non-glandular trichomes. Because of this additional water demand, the frequency of plants with glandular trichomes may decline relative to that of plants with non-glandular trichomes as available water becomes more limiting.

INTRODUCTION

Trichomes, or plant hairs, are found on aerial parts of plants in a multitude of forms. This diverse group of structures can be arbitrarily subdivided into glandular, secretory trichomes and non-glandular trichomes (Levin 1973). Among the suggested ecological functions of trichomes are maintenance of the water balance in the leaves, deflection of intense solar radiation, and protection against herbivores (Levin 1973; Ehleringer 1984; Duffey 1986). Both glandular and non-glandular trichomes have been described in several genera within the Solanaceae (Luckwill 1943; Lemke and Mutschler 1984; Gregory et al. 1986; Ogundipe 1992).

Individual plants of *Datura wrightii* Regel (Solanaceae) produce mostly (>95%) glandular trichomes or mostly (>95%) non-glandular trichomes (van Dam et al. 1999). Plants that produce glandular trichomes feel sticky when touched, while plants with non-glandular trichomes feel velvety. The difference in trichome morphology is under the control of a single Mendelian gene, with the glandular condition dominant to the non-glandular condition (van Dam et al. 1999). Hereafter, we refer to plants with non-glandular trichomes as sticky plants and plants with glandular trichomes as velvety plants. Sticky plants produce an exudate composed of acyl sugar esters in water, while velvety plants do not (van Dam and Hare 1998a). These plant types grow adjacently in populations in which they co-occur, often with their branches interdigitated, indicating that microsite specialization of the types is unlikely. The trichome dimorphism is important in determining plant susceptibility to herbivores. Velvety plants are more susceptible to whiteflies and the tobacco hornworm, *Manduca sexta* (Johannson) (van Dam and Hare 1998a), but sticky plants are more susceptible to a mirid bug, *Tupiocoris notatus* (Distant) (van Dam and Hare 1998b; Elle and Hare 2000).

Previously, van Dam et al. (1999) surveyed the distribution of velvety and sticky *D. wrightii* phenotypes in 19 southern California plant populations and found that the frequency of the sticky phenotype varied from 0% to 82%. They suggested that the production of a water-based exudate by glandular trichomes might be especially costly in arid environments, thus possibly accounting for the relative scarcity of sticky plants in the deserts (van Dam et al. 1999). Here, we expand that initial survey to include a total of 56 plant populations not only from southern California, but also from coastal and inland central California as well. We also explore in more detail the potential interaction between water availability and glandular trichome production by analyzing the frequency of sticky plants as a function of overall water availability, as indexed by mean annual rainfall and mean annual evapotranspiration demand.

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[1] Author to whom correspondence should be addressed. E-mail: harejd@citrus.ucr.edu.
[2] Present Address: Dept. of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6 Canada.

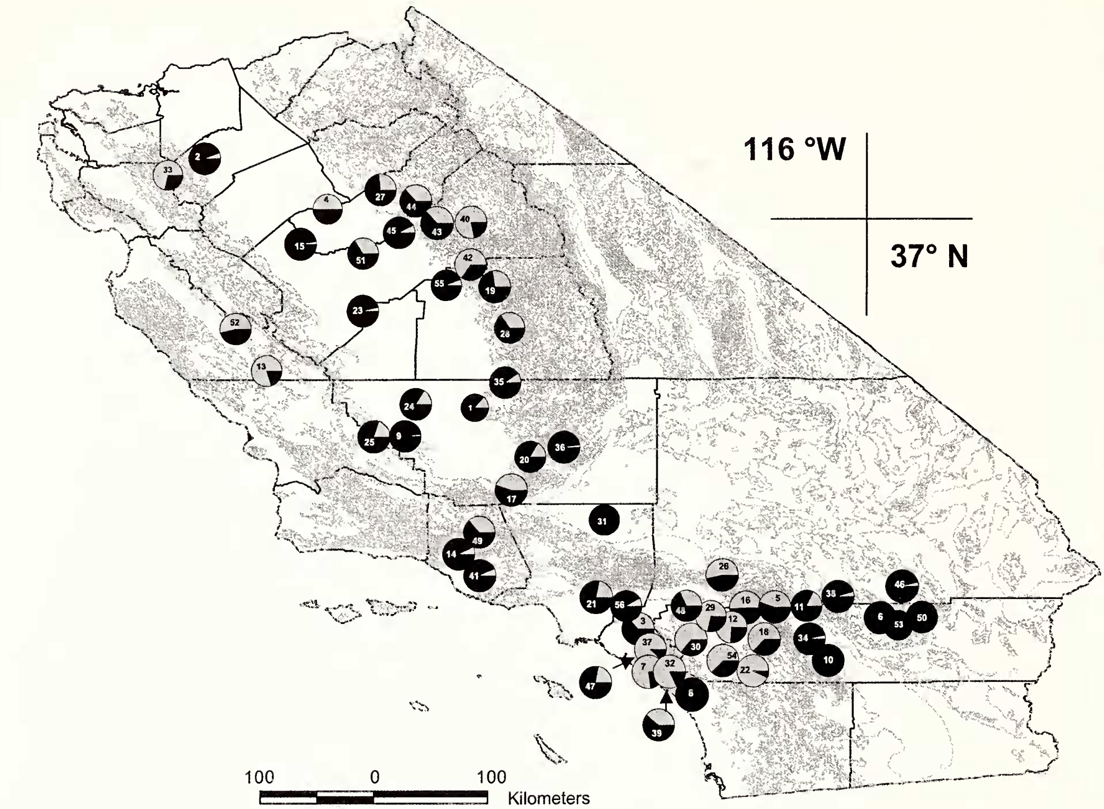

FIG. 1. Sampling locations for sticky and velvety *D. wrightii*. Frequencies of sticky plants are shown in gray, and frequencies of velvety plants are shown in black. The number within each graph refers to numbered populations described in Table 1.

MATERIALS AND METHODS

Datura wrightii is a perennial plant species found in sandy or gravelly dry places in the southwestern U.S. and Mexico (Avery et al. 1959; Munz 1973). Despite the production of large trumpet-shaped flowers, self-pollination predominates, and outcrossing rates are no more than 30% (Snow and Dunford 1961; E. Elle, personal observation).

The phenotype of plants was determined within 56 plant populations of varying size in southern and central California (Fig. 1, Table 1). The phenotype of at least 25 plants in each population was classified by touch and sight into either sticky or velvety categories. The presence or absence of glandular trichomes was confirmed with a hand lens (10×). Most populations were sufficiently small that every individual was examined. The southern California populations were censused in 1997, the San Joaquin Valley and Sierra foothill populations were censused 1998, and the central coast populations were censused in 1999. Sampling was conducted in August or September of each year to ensure that plants were expressing their adult trichome phenotype (van Dam et al. 1999).

Mean annual rainfall at each sampled location was obtained from a map of California annual precipitation published by the National Resources Conservation Services PRISM Climate Mapping Project. This map shows lines of equal mean annual rainfall (isohyets) based upon records taken from 1961 through 1990 plotted at 5 cm. Mean annual rainfall was interpolated between adjacent isohyets to the nearest 2.5 cm. Thus, mean annual rainfall is used as an index of water "supply" to all sampled sites.

An index of mean annual water "demand" that is widely used in irrigation management is "reference evapotranspiration," and is based on the amount of water that would evaporate from an open pan. Values for mean annual reference evapotranspiration (ET_0) were obtained from a map published by the California Irrigation Management Information System (CIMIS) that divides California into 18 evapotranspiration zones.

An index of overall water deficit was calculated for each site by subtracting the mean annual rainfall from the mean annual ET_0 for each site. A value of zero would indicate that mean annual rainfall equaled mean annual ET_0, while positive values would indicate that mean annual ET_0 exceeded mean annual rainfall. The relationship between the percent of plants within populations expressing the

TABLE 1. LOCATIONS OF *D. WRIGHTII* POPULATIONS SAMPLED FOR THE FREQUENCY OF TRICHOME TYPES. Populations are numbered as in Figure 1. All localities are in California.

1. 155 & 65. Roadside population near the intersection of State Highways 155 and 65, near Mile Marker # 20 on State Highway 155.
2. 33 & 152. Roadside population at the intersection of State Highways 33 and 152 near Dos Palos.
3. Arroyo Trabuco. Natural population within O'Neill Regional County Park, Orange Co.
4. Avenue 22 & Road 191/2. Natural population in an abandoned field bordering this intersection in Madera Co.
5. Banning. Roadside population south of Banning on Old Banning Road.
6. Barker Dam. Natural population, Joshua Tree National Park.
7. Bell Canyon. Natural population, Caspers Regional Wilderness Park, Orange Co.
8. Bonsall. Roadside population along State Highway 76 south of Bonsall.
9. Buttonwillow. Roadside population near the intersection of Elk Grove Road and State Highway 158.
10. Carrizo Canyon. Natural population off of State Highway 74.
11. Casino Morongo. Roadside population near this Indian casino on State Highway 62.
12. Coyote Pass. Natural population within the Lake Perris State Recreation Area.
13. Estrella Road. Roadside population north of the intersection of Estrella Road and State Highway 46.
14. Fillmore. Roadside population near the eastern city limits on State Highway 126.
15. Firebaugh. Roadside population at the intersection of State Highway 33 and Douglas Avenue.
16. Gilman Springs Road. Roadside population south of State Highway 60, approx. 0.8 mi. south on Gilman Springs Road.
17. Gorman. Roadside population on Gorman Road, approximately 2 miles east of Interstate 5.
18. Idyllwild. Natural population off State Highway 243 approximately two miles south of Idyllwild.
19. Kaweah Lake. Natural population at the Lemon Hills Recreation Area on State Highway 198.
20. Kern River Canyon. Roadside population on State Highway 178, near Call Box # 178-128.
21. La Palma. Roadside population at the intersection of La Palma Road and Huxford Avenue at the east end of Yorba Regional Park.
22. Lake Elsinore. Roadside population near the intersection of Riverside Avenue and Collier Road.
23. Lemoore. Roadside population near the intersection of Idaho Street and 19th Avenue.
24. McFarland. Weedlot population on Highway 43 directly west of McFarland in waste ground near an abandoned railroad siding.
25. McKittrick. Weedlot population near the intersection of State Highways 58 and 33.
26. Mill Creek. Natural Population at the Mill Creek Ranger Station, State Highway 38.
27. Millerton Lake. Natural population around the Millerton Historic Courthouse.
28. Milo Ranger Station. Roadside population on Yokohl Road near the Milo Ranger Station.
29. Moreno Valley. Weedlot population near the intersection of Moreno Beach Drive and Ironwood Avenue.
30. Motte. Natural population within the Motte Rimrock UC Reserve along Pictograph Trail.
31. Neenatch. Roadside population on State Highway 138 approximately midway between Pearblossom and Little Rock, 4 mi. east of the California Aqueduct.
32. Ortega Flats. Natural population in Caspers Regional Wilderness Park, Orange Co.
33. Pacheco Pass. Weedlot population off Highway 152 at Dinosaur Point boat launching ramp, San Luis Reservoir.
34. Palm Springs. Weedlot population in the vicinity of the parking lot for the Palm Springs Tram off State Highway 111.
35. Porterville Road. Roadside population north of Glenville, on Jack Ranch Road.
30. Rich Bar. Weedlot population along State Highway 178 near the Rich Bar Overflow parking lot.
37. Riley Wilderness. Natural population within Riley Wilderness Park, Orange Co.
38. Route 62. Roadside population 2 miles east of the boundary of Joshua Tree National Park.
39. San Onofre. Roadside population along Interstate 5.
40. Sequoia National Forest. Roadside population along State Highway 180 approximately 1 mile inside National Forest boundary.
41. Simi Valley. Weedlot population at Los Angeles Avenue and Angus Road.
42. Three Rivers. Natural population in a field on North Fork Road 4.8 miles from State Highway 198.
43. Tollhouse Grade. Roadside population on Tollhouse Road at the Sierra National Forest boundary.
44. Tollhouse Road. Roadside population between Humphrey's Station and Tollhouse.
45. Trimmer Springs Road & Belmont Avenue. Roadside Population at intersection.
46. Twentynine Palms. Roadside population near the intersection of Utah Trail and Underhill Road near the north entrance to Joshua Tree National Park.
47. UC Irvine. Weedlot population in an undeveloped field near University Avenue and Beech Tree Road.
48. UC Riverside. Natural population within the UC Riverside Botanic Gardens grounds.
49. Val Verde. Population in an abandoned field on San Martinez Road off State Highway 126 near Val Verde County Park.
50. White Tank. Natural population within Joshua Tree National Park.
51. Whitesbridge Road. Roadside population on State Route 180 near Mendota.
52. Wild Horse Road. Weedlot population in an abandoned field south of King City, east of U.S. 101.
53. Wilson Canyon Wash. Natural population within Joshua Tree National Park.
54. Winchester Road. Weedlot population on undeveloped ground near the intersection of Winchester Creek Road and State Highway 79.
55. Woodlake. Natural population along a stream on Highway 245 directly east of the Woodlake Airport.
56. Yorba Linda. Weedlot population on a vacant lot near Weir Canyon Road and Savi Ranch Road.

sticky phenotype and mean annual water deficit was determined by linear regression analysis.

Results and Discussion

The frequency of sticky plants varied from 0% in six populations, mostly from the Mojave Desert, to 93% in a population near Lake Elsinore. Other plant populations having more than 75% sticky individuals included two populations from the coastal mountains of Orange County (Ortega Flats and Riley Wilderness State Park), one from the mountains of the central Coast Range (Estrella Road), and another from the foothills of the central Sierra Nevada range (Sequoia National Forest).

Mean annual precipitation from these sites ranged from a low of 10 cm annually at the Twentynine Palms population in the Mojave Desert to a high of nearly 69 cm annually at the Idyllwild population in the San Jacinto Mountains. Sites where rainfall also averaged 15 cm or less include all of the Mojave Desert populations as well as populations in the southwestern portion of the San Joaquin Valley (McKittrick, Buttonwillow). Other populations where mean annual rainfall was relatively high (50 cm or more) were limited to other areas in the foothills of the Sierra Nevada mountain range (Porterville Road, Milo Ranger Station, Tollhouse Road, Tollhouse Grade, and Sequoia National Forest) or the base of the San Bernardino Mountains (Mill Creek).

Highest mean annual ET_0 (183 cm, Zone 18) occurred in the two populations in the Coachella Valley (Carrizo Canyon, Palm Springs), followed by the three populations in Joshua Tree National Park (Barker Dam, White Tank, Wilson's Creek, 168 cm, Zone 17), and the two populations from the floor of the San Joaquin Valley in Fresno Co. (Whitesbridge Road, Lemoore, 157 cm, Zone 16). Lowest mean annual ET_0 occurred in the San Onofre population (Zone 1, 84 cm), followed by the populations on the coastal plain of Orange and San Diego Counties (UC Irvine, Bonsall), and at the base of the Santa Ana Mountains in Orange County (Arroyo Trabuco, Bell Canyon, Ortega Flats, Riley Wilderness, Zone 4, 118 cm).

Overall, the percentage of sticky plants was positively correlated with increasing mean annual rainfall ($r = 0.455$, $P = 0.004$, $n = 56$) and negatively correlated with increasing mean annual ET_0 ($r = -0.474$, $P = 0.0002$, $n = 56$). Mean annual ET_0 and mean annual rainfall were significantly, but imperfectly negatively correlated ($r = -0.32$, $P = 0.016$, $n = 56$), so that when the two variables were combined into the new variable, "mean annual water deficit," the percentage of sticky plants declined with increasing water deficit, ($r = -0.572$, $P < 0.0001$, $n = 56$), and water deficit accounted for 33% of the variation in the percentage of sticky plants (Fig. 2). These results suggest that sticky plants may be at a selective disadvantage in relatively dry environments because glandular trichomes may impose an additional water demand on sticky plants, as has been found for at least one other plant species (Lauter and Munns 1986).

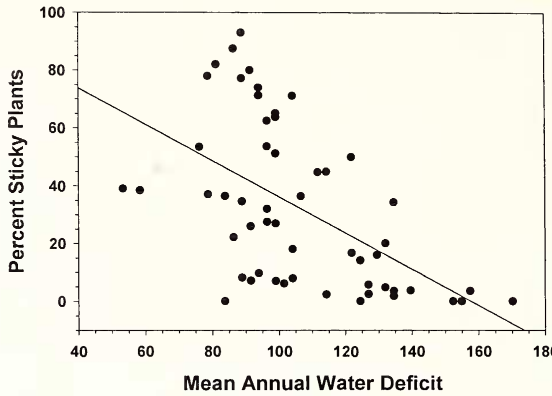

Fig. 2. Percent of sticky plants in each population as a function of water deficit. Water deficit was calculated as the mean annual rainfall at each site subtracted from the mean annual evapotranspiration (ET_0) at each site. Regression equation: Percent sticky = 98.90 − (0.6370 * water deficit); $P < 0.0001$, $n = 56$).

The low proportion of variance in the frequency of sticky plants that is accounted for by water supply (rainfall) and demand (ET_0) suggests that other factors may also influence the frequency of sticky plants in particular locations, and we know from previous studies that trichome morphology strongly influences the susceptibility of plants to insect attack (van Dam and Hare 1998a, 1998b; Elle et al. 1999; Elle and Hare 2000). Within sites of equivalent water availability, natural selection may favor sticky plants over velvety plants when the herbivore community is dominated by species such as whiteflies, flea beetles, and *M. sexta* and disfavor sticky plants when the herbivore community is dominated by species like *T. notatus* that are particularly well adapted to feed on plants with glandular trichomes (Elle and Hare 2000). Thus, a portion of the remaining variation in trichome frequencies could be accounted for by variation in the structure of herbivore communities attacking plant populations in areas of similar water availability. Such variation in herbivore community structure has already been shown for different populations within southern California habitats (Elle and Hare 2000).

Additionally, because these plant populations also are relatively small, and self-pollination predominates (Snow and Dunford 1961), founder effects and limited gene flow among plant populations may also contribute to variation in phenotype frequencies among plant populations with similar water availability. In order to completely account for all of the variation in trichome frequencies among these plant populations, it would be necessary to consider the actual site-specific water availability, the pattern and magnitude of damage by insect species differentially adapted to trichome type, and the ability of plant populations to respond genetically to natural selection by these factors. Nevertheless, the data presented here suggest that variation in the availability of water, as indexed by variation in mean annual rainfall and mean annual evapotranspiration, may provide a broad gradient of resource availability upon which more specific interactions between *D. wrightii* trichome types and both biotic and abiotic components of the plant's local environments are displayed.

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